RESEARCH ARTICLE

Assessing behaviour states of a forest carnivore in a road-dominated landscape using Hidden Markov Models

Eduardo M. Ferreira[1,2*], Francesco Valerio[1,2,3*], Denis Medinas[2,4], Nelson Fernandes[2], João Craveiro[2], Pedro Costa[2], João Paulo Silva[4], Carlos Carrapato[5], António Mira[1,2], Sara M. Santos[1,2]

1 MED – Mediterranean Institute for Agriculture, Environment and Development, University of Évora. Mitra, 7002–554 Évora, Portugal 2 Conservation Biology Lab, Department of Biology, University of Évora, Évora, Portugal 3 EaRSLab – Earth Remote Sensing Laboratory, University of Évora, 7000–671, Évora, Portugal 4 CIBIO/InBIO – Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Universidade do Porto, Campus Agrário de Vairão, 4485–601 Vairão, Portugal 5 ICNF/PNVG – Instituto de Conservação da Natureza e Florestas/Parque Natural do Vale do Guadiana, Mértola, Portugal

Corresponding author: Eduardo M. Ferreira (ferreiraeduardo.mr@gmail.com)

Abstract

Anthropogenic infrastructures and land-use changes are major threats to animal movements across heterogeneous landscapes. Yet, the behavioural consequences of such constraints remain poorly understood. We investigated the relationship between the behaviour of the Common genet (*Genetta genetta*) and road proximity, within a dominant mixed forest-agricultural landscape in southern Portugal, fragmented by roads. Specifically, we aimed to: (i) identify and characterise the behavioural states displayed by genets and related movement patterns; and (ii) understand how behavioural states are influenced by proximity to main paved roads and landscape features. We used a multivariate Hidden Markov Model (HMM) to characterise the fine-scale movements (10-min fixes GPS) of seven genets tracked during 187 nights (mean 27 days per individual) during the period 2016–2019, using distance to major paved roads and landscape features as predictors. Our findings indicated that genet's movement patterns were composed

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* These authors contributed equally to this work.

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of three basic behavioural states, classified as "*resting*" (short step-lengths [mean = 10.6 m] and highly tortuous), "*foraging*" (intermediate step-lengths [mean = 46.1 m] and with a wide range in turning angle) and "*travelling*" (longer step-lengths [mean = 113.7 m] and mainly linear movements). Within the genet's main activity-period (17.00 h-08.00 h), the movement model predicts that genets spend 36.7% of their time travelling, 35.4% foraging and 28.0% resting. The probability of genets displaying the travelling state was highest in areas far away from roads (> 500 m), whereas foraging and resting states were more likely in areas relatively close to roads (up to 500 m). Landscape features also had a pronounced effect on behaviour state occurrence. More specifically, travelling was most likely to occur in areas with lower forest edge density and close to riparian habitats, while foraging was more likely to occur in areas with higher forest edge density and far away from riparian habitats. The results suggest that, although roads represent a behavioural barrier to the movement of genets, they also take advantage of road proximity as foraging areas. Our study demonstrates that the HMM approach is useful for disentangling movement behaviour and understanding how animals respond to roadsides and fragmented habitats. We emphasise that road-engaged stakeholders need to consider movement behaviour of genets when targeting management practices to maximise road permeability for wildlife.

Introduction

Movement behaviour is a key characteristic of animal species, dictating how, when and why individuals move through landscape in order to access resources, mates and seek safety from predators and disturbance, along with other activities (e.g. migration) at various spatio-temporal scales (Nathan et al. 2008; Wittemyer et al. 2019). Movement underpins variation in individual fitness, affecting populations' dynamics (e.g. species interactions and distribution) and is essential for long-term population persistence (e.g. gene flow; Morales et al. 2010). As such, the survival and persistence of animal species depend on the success of their movements across landscapes, especially anthropogenic landscapes (Tucker et al. 2018). Human activities (e.g. agriculture and urbanisation) are the main drivers of landscape fragmentation and habitat loss worldwide (Venter et al. 2016), thus impacting animal movement. High quality habitats are frequently dissected into small patches, surrounded by unsuitable habitat and anthropogenic features, such as roads (e.g. van der Ree et al. 2015). As a result, species are forced to move between isolated patches of suitable habitat within an often inhospitable matrix, posing constraints on their movement decisions and, ultimately, on their survival chances (e.g. roadkill; McCall et al. 2010; Basille et al. 2013).

Roads are one of the most important causes of habitat fragmentation worldwide. Roads have multiple negative impacts on terrestrial wildlife populations (Barrientos et al. 2021), namely through increased wildlife mortality (Ascensão et al. 2014; Grilo et al. 2018), hampering ecological connectivity (Carvalho et al. 2016; Chen and Koprowski 2016; Ascensão et al. 2017) or affecting species activity and individual behaviour (e.g. Kociolek et al. 2011; Medinas et al. 2019). Some traits make certain species more

vulnerable to road impacts than others (Rytwinski and Fahrig 2012). Given their wide-reaching home ranges and dispersal needs, medium and large-sized carnivores are more likely to encounter a road on their daily movements and, consequently, have higher probability of being road-killed (Rytwinski and Fahrig 2012; Tucker et al. 2018). On the other hand, if they avoid the road, gene flow between populations on both sides of the road may be reduced in the long term, leading to an increased extinction risk (e.g. Holderegger and Di Giulio 2010). Whereas the impacts on mortality and connectivity have been examined in literature (Rytwinski and Fahrig 2013; Teixeira et al. 2020), the consequences on wildlife behaviour from the presence/proximity of roads are scarcely addressed. Road-dominated environments can prompt different behavioural responses, wherein species may exhibit different movement patterns, depending on their sex, age, life-history and landscape context (e.g. Ascensão et al. 2016; Carvalho et al. 2018). Certain species, for example, tend to avoid or move faster in poor habitat quality areas and in proximity of roads (Carvalho et al. 2016; Gaston et al. 2016). On the other hand, roads can promote foraging areas that are highly attractive to a variety of predator species (Barrientos and Bolonio 2008; Silva et al. 2019). Thus, it is critical for road mitigation planning to understand how road proximity and landscape conditions affect behaviour patterns of mammal carnivores, as these can influence the effectiveness of mitigation outcomes (e.g. Scrafford et al. 2018; Zeller et al. 2019).

Despite the evident role of behaviour on animal movement (Nathan et al. 2008), movement analyses that consider the effects of behaviour are still uncommon and remain a key challenge in ecology (Zeller et al. 2012; McClintock et al. 2020). Traditionally, animal movement responses to roads and landscape context have been quantified by analysing telemetry-based data as a function of extrinsic factors (e.g. habitat composition, daily period), while disregarding behaviour effects. Nevertheless, animal movement paths are composed of a mixture of underlying behavioural states, characterised by specific and unique signatures (Nathan et al. 2008; Wittemyer et al. 2019). These behavioural states are adopted by animals in response to environmental gradients and biological needs, dictating observed movement patterns (van Beest et al. 2019; Farhadinia et al. 2020). Due to recent advances in analyses, it is now possible to describe the mechanisms underlying animal movement, allowing for a more explicit assessment of the influence of animal behaviour on movement patterns (e.g. Gardiner et al. 2019). One flexible tool is the Hidden Markov Model (**HMM**), which allows the interpretation and classification of behavioural states from movement data, depending on the specific characteristics of individual movement paths (Patterson et al. 2017; McClintock et al. 2020).

Here, we studied the relationship between the movement behaviour of a Mediterranean forest carnivore, the common genet (*Genetta genetta*) and road proximity within an open dominant forest landscape in southern Portugal, included in an area fragmented by roads. We used a multivariate Hidden Markov Model (HMM) applied on fine-scale GPS data. Specifically, we aimed to: (i) identify and characterise the behavioural states displayed by genets; and (ii) understand how behavioural states are affected by proximity to roads and landscape predictors. The genet was selected as a model species because, as a carnivore, its low population density and large home range make it vulnerable to the effects of road and habitat fragmentation (Rytwinski and

Fahrig 2012; Ceia-Hasse et al. 2017). Genets are widespread through Mediterranean areas, are semi-arboreal and move preferentially within forest patches with dense shrub vegetation cover and close to riparian habitats (Camps and Alldredge 2013; Carvalho et al. 2016; Grilo et al. 2016). In addition, previous studies have shown that this carnivore is often road-killed (Grilo et al. 2009; Carvalho et al. 2018) and that movements and space use are constrained by roads (Galantinho and Mira 2009; Carvalho et al. 2016; Carvalho et al. 2018). However, information is scarce on their behavioural patterns at fine scale when close to roads, this information being fundamental when planning road mitigation measures.

Methods

Study area

Our study was carried out in the Alentejo Region, southern Portugal (38°37'24.33"N, 8°06'26.44"W; Fig. 1). We focused on the linear infrastructure corridor linking Montemor-o-Novo to Évora, which is comprised of a medium-high traffic national road (EN114; nocturnal traffic varies from 882 to 1683 vehicles/night; EP 2005), with high mortality values of genets (mean mortality rate of 12.8 individuals/100 km/ year; Carvalho et al. 2018). It also includes a section of the A6 motorway running parallel to the EN114, along with other low-traffic regional roads scattered throughout the area. The landscape is dominated by cork (*Quercus suber*) and holm oak (*Quercus rotundifolia*) stands, an agroforestry system with varying tree density, while also comprising pastures and crops. Other less representative land-cover types include olive groves, some plantations of *Pinus* spp. and *Eucalyptus* spp. and urban areas, which are scarce. The result is a fragmented landscape bisected by roads, with forest patches of varying size that are interspersed with agricultural fields and linear natural elements, such as riparian habitats. The topography is generally flat or undulating and ranges from 150 to 400 m a.s.l. The climate is Mediterranean, with mild, wet winters (average daily temperature ranging from 5.8 to 12.8 °C in January) and hot, dry summers (average daily temperature ranging from 16.3 to 30.2 °C in July). The average annual precipitation is 609.4 mm (IPMA 2020).

Genets trapping and handling

Genets were live-captured in forest patches adjacent to the EN114 road in three different sessions (December 2016, January 2018 and January 2019), each one being carried out for 2–3 weeks. We used 10–12 wire cages (Tomahawk Deluxe Single door live traps) baited with sardines and eggs, deployed in suitable genet habitats (e.g. forest with riparian or shrub areas). The traps were placed approximately 500 m apart and within 1 km from paved roads. This design of trap spacing was based on the average radius (~ 1 km) of genet home range (3.3 km²; Santos-Reis et al. 2004), to maximise animal capture.

Each captured animal was immediately transported to the Veterinary Hospital (University of Évora) where a veterinarian conducted sedation and handling of genets. Sedation was performed with a mixture of ketamine hydrochloride (100 mg ml^{-1}) (Imalgene 1000, Lyon, France) and medetomidine hydrochloride (1 mg ml^{-1}) (Domitor, Pfizer, New York, USA) (ratio 2:1 by volume) using a dosage of 0.12 ml kg^{-1} (Carvalho et al. 2014). After being weighed, sexed and observed, genets were tagged for individual identification with Passive integrated transponders (PIT; model HPT9, Biomark, Boise, USA). Genets were equipped with GPS collars: Litetrack RF-40 VHF DL (45 g), Biotrack, Dorset, UK; and low-cost GPS/GSM collars (~ 50 g), Movetech Telemetry. Only adult and/or subadult animals were collared as long as the equipment weighed less than 3.5% of the animal's body weight and if the individuals were in good health (Ossi et al. 2019). Animals were released at the point of capture in the same day after fully recovering from anaesthesia. Capture and handling procedures were in conformity with Portuguese legal regulations (658/2016/ CAPT; 659/2016/CAPT; 37/2018/CAPT; 38/2018/CAPT; 136/2019/CAPT).

Collection and processing of movement data

GPS collars were set to obtain spatial locations every 10 minutes during the period of main activity of genets (17.00 h–08.00 h). Data from the first five hours after animal collaring were discarded to ensure the lowest possible behavioural bias. In addition, we removed all spatial locations that: (1) had a dilution of precision (DOP) > 3, following Biotrack GPS collar specifications and (2) locations with DOP < 3, but potentially erroneous (e.g. within a dam or too far away within consecutive locations), considering the average positional error associated with the spatial locations (mean = 8 m; SD = 10). We also regularised the time of spatial locations to fulfil HMM assumptions – negligible measurement error and regular sampling (Michelot et al. 2016).

A night of tracking (without more than two consecutive missed locations; > 30 min) was defined as the sampling unit, thus constituting a time series of successive locations (e.g. animal path) (e.g. Gardiner et al. 2019). Isolated missing locations (NAs) were linearly interpolated in paths containing a maximum of 15% of NAs, corresponding to a maximum of one missing location per hour (23% of NAs in 49% of paths). Time regularisation and spatial interpolation of locations were performed with the R package "adehabitatLT" (Calenge 2006).

Movement data were obtained for seven genets (one female and six males) successfully tracked during 187 nights (mean 27 days per individual) between 30 November 2016 and 29 March 2019, temporally spanning the species breeding season (Carvalho et al. 2018).

Road and landscape predictors

We calculated a set of important explanatory predictors for genet movement in the same landscape (Carvalho et al. 2016). Thus, six predictors reflecting road proximity, land cover, forest configuration and habitat productivity were considered (Table 1). The Euclidean distance of the genet locations to the nearest major paved road ("Road") was

Table I. Description and source of the environmental predictors used for HMM models.

Code	Description	Predictor type	Median (min – max)
Road	Distance to the nearest main paved road (m)	Anthropogenic features	461.0 (0.0–1978.0)
DForest	Distance to the nearest forest patch (m)	Landscape features	6.3 (0.0–690.9)
ForestED	Density of forest edges (m/ha) in a buffer of 100 m	Landscape features	229.0 (0.0–627.1)
ForestPS	Mean patch size of forest habitats in a buffer of 100 m (ha)	Landscape features	2.0 (0.0–3.3)
Riparian	Distance to the nearest riparian habitat (m)	Landscape features	176.6 (0.0–1290.0)
Product	Habitat productivity measured in a 100 m pixel	Landscape features	0.4 (0.1–0.7)

calculated from the OpenStreetMap geospatial data repository (OpenStreetMap 2020). Agroforestry land-use classes (Level 1) were extracted from the Portuguese land-cover "Carta de Ocupação do Solo" product (COS 2018), on which the forest configuration variables, "DForest", "ForestED" and "ForestPS" were calculated. "DForest" was calculated from the Euclidian distance to forests, while the latter two predictors were calculated using the metrics of edge density ("ForestED") and patch size ("ForestPS"), from FRAGSTATS v.2.0 software (McGarigal et al. 2012). Distance to riparian habitats ("Riparian") was obtained after the intersection of the stream layer with the tree density layer from the EU-Hydro and Tree Cover Density products, respectively, both retrieved from the Copernicus Land Monitoring Service (Copernicus 2020). Moreover, we also calculated an additional predictor, habitat productivity ("Product"), following Oeser et al. (2019), a proxy of resource availability for genets, as similarly explored in other studies for other mammals (Carter et al. 2019; Beumer et al. 2020). Habitat productivity was derived from Landsat-8 Operational Land Imager (OLI) using the Level-1 collection of atmospherically-corrected imageries through the Google Earth Engine cloud platform (Gorelick et al. 2017). This remote sensing predictor was calculated to reflect the habitat productivity at the time the movement was sampled, thus reflecting high temporal and spatial precision of habitat conditions. For this purpose, we derived the Tasseled Cap greenness metric by transforming the Landsat multispectral bands (Crist and Cicone 1984; Oeser et al. 2019). We further applied the median and a normalisation procedure to the calculated time-series metrics. Such procedure temporally reflected the exact period when each individual genet was sampled, from December to January (see above) (Grilo et al. 2009; Carvalho et al. 2018).

The predictors, not based on distances, were upscaled to 100 m (Carvalho et al. 2016; Valerio et al. 2019). We appended the raster values of all predictors to the genet spatial locations using the R package "raster" in R (Hijmans and van Etten 2012).

Data analysis

Behavioural states of the genets were inferred using HMM from movement data. We developed HMMs by modelling step length with a gamma distribution and turning angles using a von Mises distribution – a circular analogue of the normal distribution (Michelot et al. 2016). We considered HMMs with three behavioural states, since 3-state models are usually statistically well-supported and biologically meaningful in studies involving terrestrial mammals (e.g. Gardiner et al. 2019; Farhadinia et al. 2020). Furthermore, to

ensure optimisation of Maximum Likelihood (numerical stability), we ran 50 HMMs trials with different sets of randomly chosen starting values within a range of plausible values (Michelot and Langrock 2019), determined by inspecting histograms of step length and turning angles (Michelot et al. 2019). We found that model output was robust to different sets of starting values, reflecting a converging value of Maximum Likelihood. We therefore used the average values applied in the trials to construct the null model, still confirming that it led to the same convergence value of Maximum Likelihood.

To assess the influence of roads and landscape features on behavioural state occupancy, we used explanatory predictors in the transition probabilities of the state process (Farhadinia et al. 2020). The predictors were standardised before fitting the models to ensure numerical stability and were previously tested for collinearity ($r <$ 0.7) for all pairs of predictors, so no collinearity was found. We first applied univariate models, testing one predictor at a time through Akaike Information Criterion (AIC; Akaike 1973), then comparing the AIC values with the AIC of the null model (e.g. van Beest et al. 2019; Gardiner et al. 2019). Only predictors whose univariate models showed an AIC improvement higher than five over the null model were retained for further analysis. After this screening, a forward selection procedure was used to assess the influence of the retained predictors. We again used AIC for multivariate analysis to select the best ranked and most parsimonious model from the candidate models (Burnham and Anderson 2002). To validate the best model, we examined the goodness-of-fit using the pseudo-residuals (Michelot et al. 2019). Finally, we applied the "Viterbi" algorithm to predict the most likely sequence of states (e.g. van Beest et al. 2019), hence assigning a state to each observation in the input dataset and calculating the probabilities of genets occupying the different behavioural states as a function of each predictor. Additionally, for the predictors included in the best model, we calculated the median values of all GPS locations to obtain a reference value of each predictor. Owing to the small sample size for females (one tracked animal), the two sexes were merged into HMM models. The movement models were fitted with the R package "moveHMM" (Michelot et al. 2016).

Results

Overall results

The average number of tracking days ranged from 7 to 66 days per individual (mean = 27 days), with an average number of 1058 locations per individual (Table 2).

We fitted five 3-state HMMs with different predictor dependencies on transition probabilities. The predictor "DForest" was excluded in the initial screening procedure. The forward selection procedure indicated that the HMM with five predictors produced the best model (the lowest AIC value; Table 3). Inspection of the model pseudo-residuals revealed that the goodness-of-fit was good both for step length and turning angle, with no significant evidence of lack of fit or autocorrelation problems (Suppl. material 1: Fig. S1). Thus, we focused on the movement patterns, state-allocation and predictor effects derived from this full model.

Table 2. Details of seven genets tracked in southern Portugal (Évora). For each individual, we provide detailed information about sex, age class, body weight, capture year, beginning and end date of tracking, the number of tracking days and number of GPS locations.

ID animal	Sex	Age	Weight (g)	Year	Tracking start	Tracking end	Tracking days	GPS locations
C	M	Adult	1500	2016	30/11/2016	09/12/2016	10	548
E	M	Adult	1800	2018	08/01/2018	16/01/2018	9	179
F	M	Adult	1500	2018	03/01/2018	10/01/2018	8	236
H	M	Sub-adult	1300	2019	15/01/2019	05/03/2019	50	1444
I	M	Sub-adult	1250	2019	19/01/2019	25/01/2019	7	175
J	F	Adult	1700	2019	23/01/2019	29/03/2019	66	3058
L	M	Sub-adult	1160	2019	31/01/2019	08/03/2019	37	1765
mean			1459				27	1058
sd			237				24	1091

Table 3. Summary of the log-likelihood, AIC and ΔAIC values for the tested HMM. The ΔAIC is the difference of Akaike Information Criterion between each model and the best model, indicated in bold.

Model	Log-likelihood	AIC	ΔAIC
ForestED + Riparian + Road + Product + ForestPS	-39209.41	**78518.81**	0.00
ForestED + Riparian + Road + Product	-39225.78	78539.57	20.76
ForestED + Riparian + Road	-39239.44	78554.88	36.07
ForestED + Riparian	-39256.19	78576.39	57.58
ForestED	-39273.62	78599.24	80.43
Null model (no predictors)	-39303.05	78646.10	127.29

Behaviour state-allocation

The best HMM indicated that genets' movement patterns were composed of three behavioural states (Fig. 2): state 1 with short step-lengths (mean = 10.56 m) and high turning angles (undirected movement; mean = -3.13); state 2 having medium step-lengths (mean = 46.09 m) and a wide range in turning angle (mean = 0.09), though smaller than state 1 and with low concentration, indicating a mix of tortuous movements with forward movements; state 3 included larger step-lengths (mean = 113.74 m) and turning angles highly concentrated around zero (mean = -0.01), indicating mainly fast and linear movements. The three behavioural states (1, 2 and 3) are consistent with "*resting*", "*foraging*" and "*travelling*", respectively. Within the main activity-period (17.00 h-08.00 h), the movement model predicts that genets spend 36.7% of their time travelling (range: 6.9–61.5%), 35.4% foraging (range: 20.4–54.3%) and 28.0% resting (range: 14.5–40.3%; Suppl. material 1: Fig. S2). Genets are, thus, actively moving 72% of their night-time, either foraging or travelling.

State occupancy in relation to predictors

The occurrence of the three behavioural states was best explained by "ForestED", "Riparian", "Road", "Product" and "ForestPS", outperforming all other models which presented ΔAIC values > 20 (Table 3). "Road" was found to be the third most
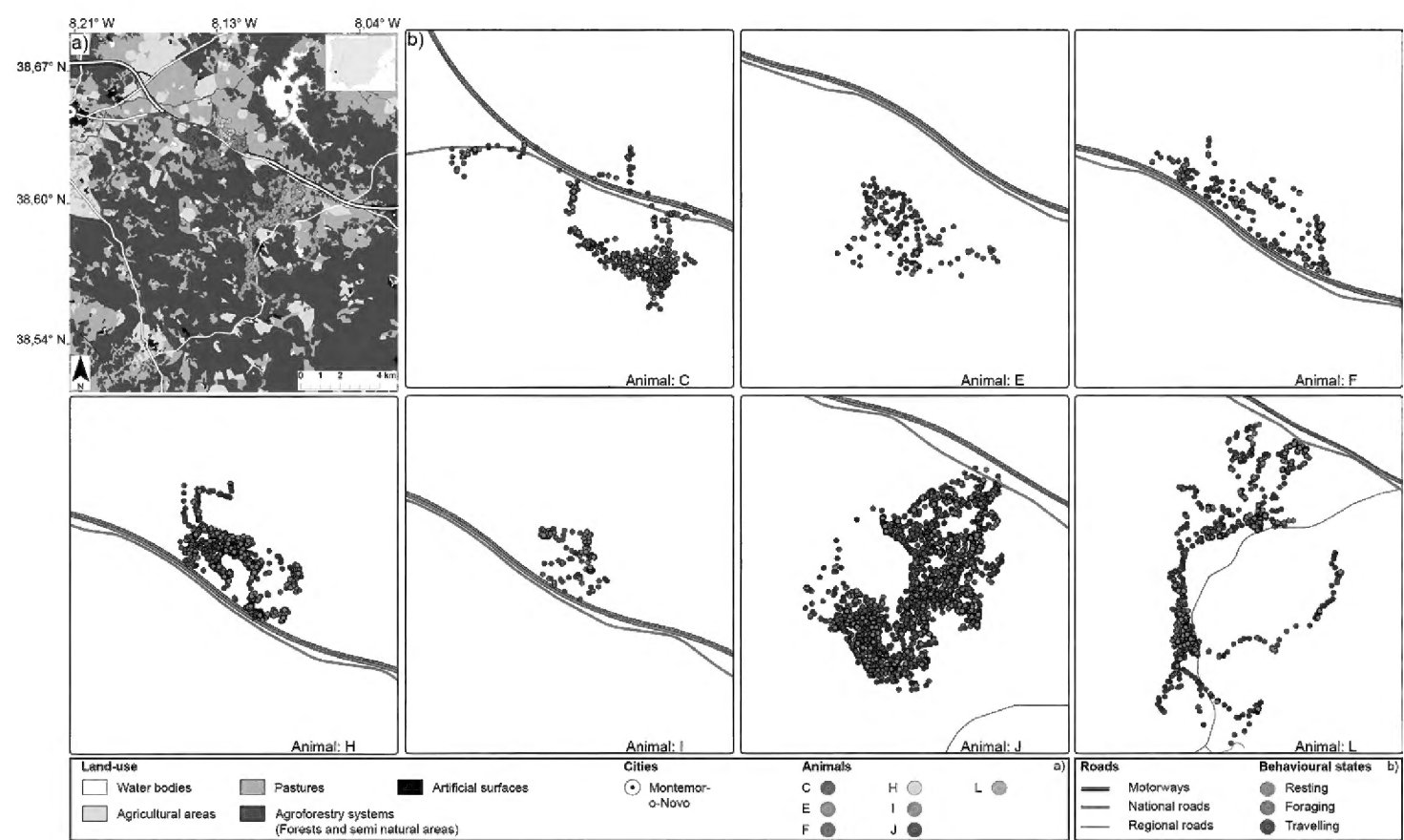
Figure 1. Location of the study area, showing all genet's locations (**a**) and locations of each radio-tracked individual, colour coded by their corresponding state (**b**). Yellow is resting (state 1), blue is foraging (state 2) and green is travelling (state 3).
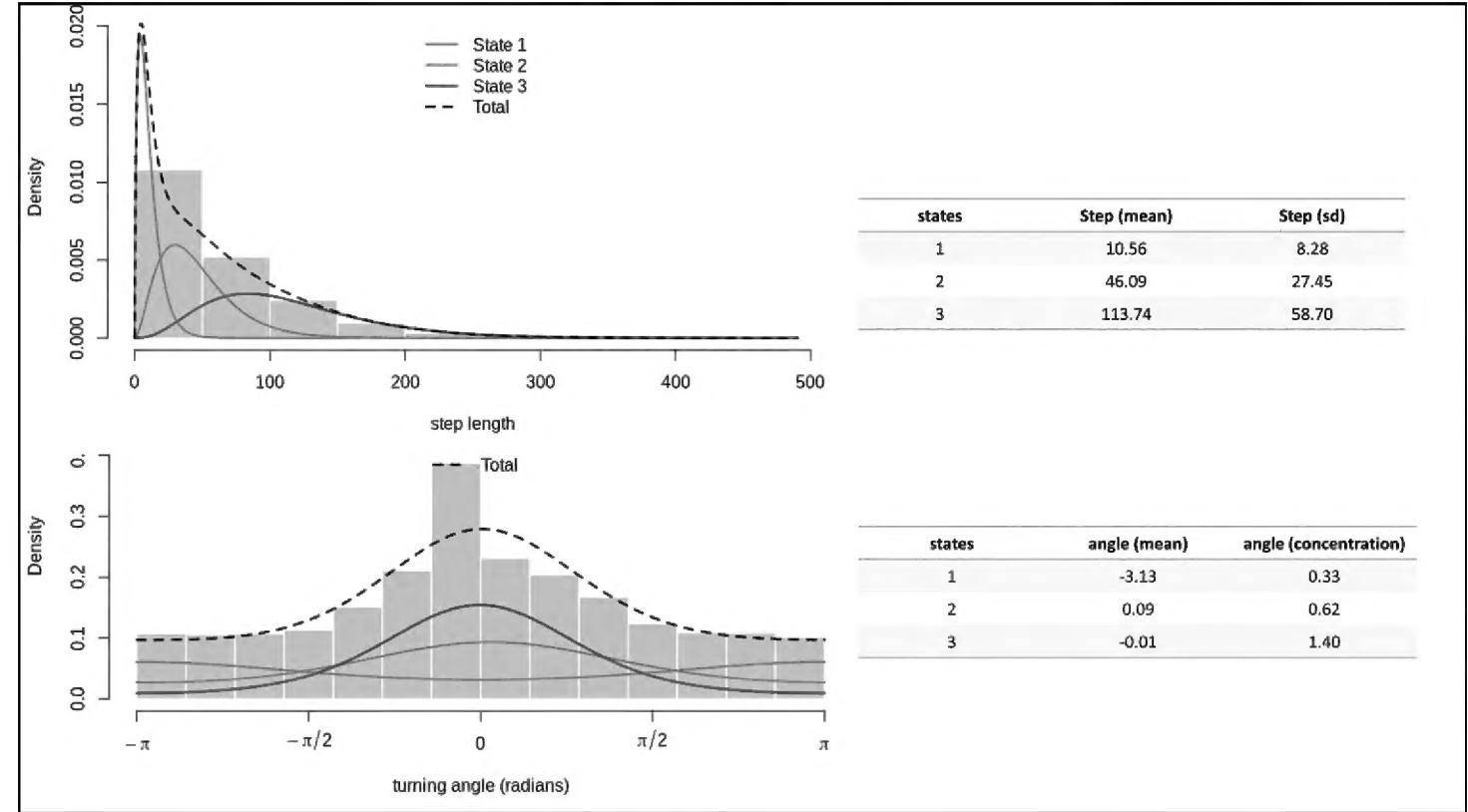

Figure 2. Histograms of observed step lengths (upper plot) and turnings angles (lower plot) with fitted distributions derived from a three-state model for all tracked genets. The coloured lines represent the estimated densities in each state, while the dashed black line is their sum. Tables included in the panels provide estimates of mean step length and standard deviation (sd) and mean turning angle and angle concentration, for observed step lengths (upper table) and turnings angles (lower table). States are: 1 = resting, 2 = foraging, 3 = travelling.

important predictor on the state probability (ΔAIC = 25.66; Table 4). The probability of genets exhibiting the "*travelling*" state was highest in areas far away from roads, whereas "*foraging*" and "*resting*" states were more likely in areas close to roads (Fig. 3). Accordingly, considering the median distance of all GPS locations to roads (461 m), when genets moved beyond that threshold, the "*travelling*" state is predicted for 46.6% of the time, becoming the dominant behavioural state (Suppl. material 1: Fig. S2). In contrast, when moving within 461 m from roads, the "*resting*" or "*foraging*" state are predicted for most of the time (42% and 31% for "*foraging*" and "*resting*", respectively). Landscape predictors also had a pronounced effect on behaviour state occurrence, particularly "ForestED" and "Riparian" and, to a lesser extent, "Product" (Tables 3, 4). "ForestPS" contributed to the final model, but its effect was less clear (Fig. 3). Furthermore, "*travelling*" had highest probability to occur in areas with lower forest
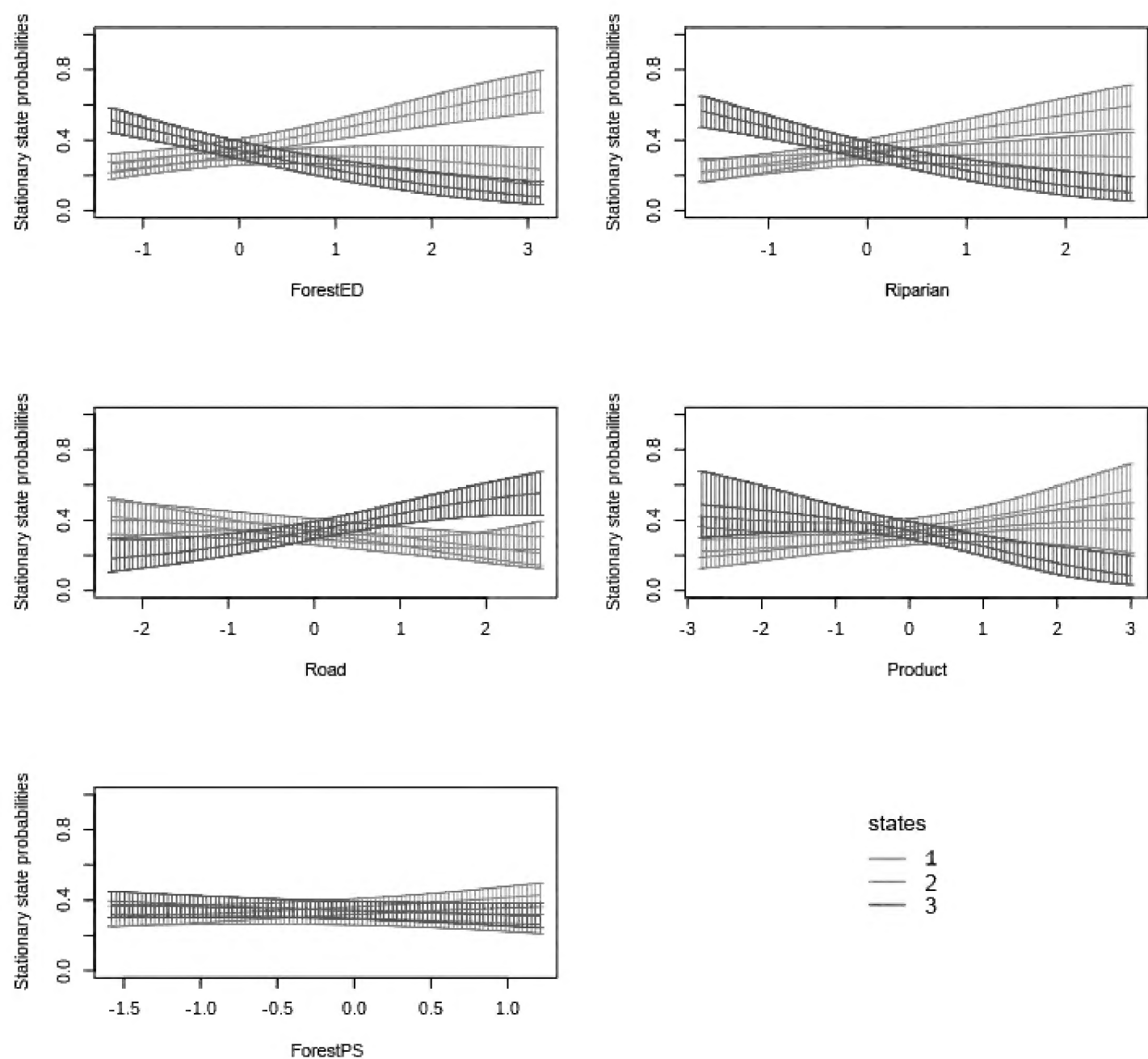

Figure 3. Stationary state probabilities (with 95% confidence intervals) as a function of each predictor considered in the best HMM model (from upper left to the right: ForestED, Riparian, Road, Product and ForestPS). States are: 1 = resting, 2 = foraging, 3 = travelling.

Table 4. Summary of the log-likelihood, AIC and ΔAIC values for the full model and for the set of models that included all, except one predictor, testing the relative importance of each predictor in the full model (the higher the ΔAIC, the higher relative importance of the predictor in explaining genet behaviour states).

Model	Log-likelihood	AIC	ΔAIC
Full model	-39209.41	**78518.81**	0.00
- ForestED	-39237.30	78562.61	43.80
- Riparian	-39233.79	78555.58	36.77
- Road	-39228.24	78544.47	25.66
- Product	-39225.91	78539.82	21.01
- ForestPS	-39225.78	78539.57	20.76

edge density (lower than 229 m/ha) and close to riparian habitats (less than 176 m), while "*foraging*" was most likely to occur in areas with higher forest edge density, while far away from riparian habitats and in more productive areas (Fig. 3). The "*resting*" state also had the highest probability of occurrence in areas with high forest edge density and far away from riparian habitats, although it was less frequent than the "*foraging*" state (Fig. 3). The overlap of areas for state probabilities as a function of "ForestPS" (and, to a lesser degree, "Product") suggests that, although contributing to the final model, these predictors have a minor influence on the occurrence of genet behavioural states (Fig. 3).

Discussion

Hidden Markov Models are used in our study to distinguish the behaviours of a small forest carnivore in an area crossed by a main road and highway corridors. We were able to infer three behavioural states (resting, foraging and travelling) using data from movement paths collected at fine spatiotemporal scales. Changes between states were influenced by distance to roads, but forest edge density and distance to riparian habitats also had a stronger effect, while the productivity habitat metric played a role as well.

Overall, our findings shed light on how genets make decisions about roads and landscape features, specifically their perception of road vicinities. To our best knowledge, this is a novel approach to road ecology applied to carnivores. We discuss the behavioural states identified, as well as the insights gained for road mitigation planning.

Are roads a behavioural barrier to genets or a resource provider?

Roads can be very attractive to carnivores because they offer food resources and easier travel routes (Bateman and Fleming 2012; Zimmermann et al. 2014; Dickie et al. 2016; Andersen et al. 2017). Road verges, in particular, can attract prey by providing them with vegetation cover, very often unavailable in surrounding areas (Ascensão et al. 2012; Silva et al. 2019; Galantinho et al. 2020; Valerio et al. 2020).

Our fine-scale results indicate that, in areas close to roads, the dominant types of behaviour by genets are foraging and resting, while in areas further away from roads, the travelling behaviour is more frequent. This suggests that animals use road verges and adjacent areas (< 500 m) for feeding, but not as travel routes. The resting state includes true resting sites (see Carvalho et al. 2014), but may also include short-term pauses in foraging periods, a slowdown in movement when approaching prey or a perception of a danger (e.g. road noise and light). The association of foraging behaviour with road proximity might be explained by the higher and denser vegetation in verges when compared to adjacent farmland which is commonly explored for cattle grazing, removing the refuge given by the shrub layer (Ascensão et al. 2012; Silva et al. 2019; Galantinho et al. 2020). Thus, the maintenance of shrub strata in road verges provides some benefits for certain prey species (Ascensão et al. 2015), which then attracts genets to search for food in road verges and edge habitats. This is in line with recent data suggesting that predators are attracted to road verges due to the higher prey abundance (Barrientos and Bolonio 2008), particularly small mammals (Ascensão et al. 2015; Silva et al. 2019). Indeed, genets, beyond berry tree fruits, prey mainly on small vertebrates, frequently the wood mouse (Virgós et al. 1999; Rosalino and Santos-Reis 2002; Barrientos and Virgós 2006) which is abundant in road verges even when these are embedded in forested areas (Galantinho et al. 2020).

Furthermore, our results also highlight that night-time resting behaviour is more likely in areas close to roads. This finding conflicts with other studies that, although based on gravel roads, refer other carnivores, such as African wild dogs and wolves, to avoid using road proximities when resting (Zimmermann et al. 2014; Abrahms et al. 2016). In addition, our results concern the time period when genets are most active (night-time) and our resting state should be viewed differently, as it also includes movement pauses of short time duration (less than an hour). In our study, it is likely that active foraging states alternate with movement pauses, including ambushing behaviour before catching prey. Nevertheless, the resting state also includes the typical resting behaviour in trees, commonly used in the study area (at an average height of 3 m; Carvalho et al. 2014). It is, thus, possible that the disturbance caused by the proximity of roads might be compensated by the shelter provided by the tree height from human activities and predators (Carvalho et al. 2014).

Previous results, based on telemetry, have shown that the space use and movements of genets are constrained by the presence of roads, with home ranges bordered by them (Carvalho et al. 2018). This suggests the existence of a behavioural avoidance towards roads, although the local genet population does not present genetic structuring (Carvalho et al. 2018). Our results support these conclusions (a barrier effect associated with roads), as the radio-tracked individuals in our study concentrated their movements on one side of the road corridor (national road and highway) and rarely crossed it. From the radio-tracked animals in the present study, only one adult male (animal C) crossed both the national road and the parallel highway, quickly returning to the regularly used side of the road. When exploring the other side of the highway, only foraging and travelling states were predicted. Thus, our results suggest that, although

roads represent a behavioural barrier to the movement of genets, they also take advantage of the proximity of roads as foraging areas.

Interestingly, our results also show that the travelling state occurred less frequently near roads. This is a novel finding, as some studies, yet focusing on gravel roads, found that roads are selected for travelling of African wild dogs (Abrahms et al. 2016), Norwegian wolves (Zimmermann et al. 2014) and red foxes (Bischof et al. 2019). If roads are themselves a territory boundary, with infrequent visits of neighbouring conspecifics from the opposite side, then it should be more advantageous for genets, from a competition standpoint, to patrol their territory (or explore neighbourhood) in areas far away from roads. When these areas have high quality habitat, they are more likely to be attractive to other individuals and should be secured by the territory owner. Moreover, when travelling at such a distance from the road, they avoid road disturbance and reduce the roadkill risk.

Landscape influence on behaviour

Genets are known to preferentially use forest areas and riparian habitats (Matos et al. 2009; Pereira and Rodríguez 2010). Our results are in line with these findings and go even further by identifying the different types of behaviour associated with different habitat characteristics. In our study, foraging behaviour was more likely at forest edges, far away from riparian habitats and in higher productivity habitats. Forest edges may offer foraging opportunities, in more open areas, given the higher habitat suitability for small mammals, as previously mentioned for road verges. Travelling behaviour, on the other hand, had highest probability to occur in continuous forest areas and close to riparian habitats.

While the available literature suggests that forest and riparian areas are essentially used by genets for foraging (Sarmento et al. 2009; Pereira and Rodríguez 2010) and resting (Virgós et al. 2001; Sarmento et al. 2009), our models suggest that travelling was the most frequent behaviour. Our results support the role of riparian habitats as movement corridors (documenting that observed movement parameters are compatible with travelling movement) and, therefore, of significance for landscape connectivity and mitigation planning. In fact, previous results state that, despite the presence of roads decreases landscape connectivity for genets, this effect can be minimised when riparian corridors are present, given the presence of culverts that are used as road crossing structures (Carvalho et al. 2018; Craveiro et al. 2019). This corridor effect from riparian habitats is of special importance when embedded in open agricultural areas (Pereira and Rodríguez 2010; Carvalho et al. 2016). In fact, one genet (animal C) crossed the highway using two different crossing structures (a culvert and an underpass) installed in a riparian corridor.

Implications for road mitigation

To mitigate the negative effects of roads on genet populations, we must first understand the processes that affect the behavioural responses towards roads and existing mitigation (Klar et al. 2009). According to our results, culverts and underpasses

should be in close proximity to forest and riparian habitats, as those areas seem to promote travelling behaviour of genets and might be used more frequently in road crossing events. For culverts, it is important that these structures are wide or include dry ledges, as these increase the success of crossings by genets and other carnivores (Villalva et al. 2013; Craveiro et al. 2019). The implementation of effective fences along roads should also be considered, as these may help to guide movements towards road-crossing structures (Ascensão et al. 2014), while increasing safety of genets' movements on road verges.

Study limitations

Our results should be viewed as preliminary, as we used an unsupervised HMM approach and the inferred states were not validated by direct observations of the animals in the field. However, all the diurnal resting sites identified through VHF signal during daytime (when downloading movement data during daylight hours) overlapped spatially with most locations inferred as resting states in HMM. Thus, we are confident that the obtained state classification captured most of the variation in the genet movement behaviour.

A second potential limitation is related with the number of tracked individuals and sampled period. Our sample size of individual genets was relatively small, male-biased and did not cover the entire annual cycle. Space use by genets may possibly vary throughout the year as result of seasonal changing in resource availability and reproduction cycle (Camps and Llobet 2004). On the other hand, the breeding period sampled here corresponds to the season of greatest activity, since males usually explore areas beyond their usual home range in search of receptive females as these are not yet with cubs and are, therefore, not spatially restricted (Camps and Llobet 2004). The genets' breeding period also corresponds to a period of increasing abundance of their main prey, the wood mouse, before reaching maximum densities in spring, both in road and roadless areas (Galantinho et al. 2017). Thus, although we have sampled a limited portion of the annual cycle, it should clarify the main environmental constraints influencing genet behaviour. Future HMM studies covering larger and more balanced sample sizes may be able to refine these results and accommodate inter-sexual differences, along with individual and seasonal variability on movement behaviour of genets.

Conclusions

Our results support evidence that the proximity of roads, along with more heterogeneous and fragmented areas, might favour foraging opportunities for genets, though this may also increase genet exposure to road threats. We emphasise that road-engaged stakeholders need to consider the movement behaviour of genets when targeting management practices to maximise road permeability.

Author contributions

SMS, EMF and AM conceived the study; EMF, JC, NF and PC conducted fieldwork; EMF, FV and DM developed the analysis protocol; EMF and FV analysed the data; EMF, FV and SMS wrote the first manuscript draft; all authors revised the work and gave final approval for publication.

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Supplementary material I

Figures S1–S3
Authors: Eduardo M. Ferreira, Francesco Valerio, Denis Medinas, Nelson Fernandes, João Craveiro, Pedro Costa, João Paulo Silva, Carlos Carrapato, António Mira, Sara M. Santos
Data type: Images
Explanation note: Additional files regarding 1) HMM model performance, 2) percentage of state occupancy of each tracked genet, and 3) density distribution plots of behavioural states as a function of each predictor considered in analyses.
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